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OLFACTORY RECEPTION OF POTENTIAL PHEROMONES AND PLANT ODORS BY TARNISHED PLANT BUG, *Lygus lineolaris* (HEMIPTERA: MIRIDAE)

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Abstract—Olfactory reception of potential pheromones and host-plant odors by male and female tarnished plant bugs (TPBs), *Lygus lineolaris* (Hemiptera: Miridae), was investigated by utilizing electroantennogram (EAG) techniques. In general, EAGs were similar between the sexes. Among 31 compounds of seven chemical groups tested, insect-produced butyrates and host-plant-containing green leaf volatiles (GLVs) were the most active. Hexyl butyrate and (*E*)-2-hexenyl butyrate elicited greater EAGs in males than in females. Females responded with significantly greater EAGs to alcohol and aldehyde GLVs than to their acetate derivatives. Among GLVs, sexual dimorphism was also observed in response to (*E*)-2-hexenol and (*E*)-2-hexenal. Females were more sensitive to the monoterpene geraniol than were males. While nonanal was the most stimulatory compound tested, no sexual differences in EAGs to this compound were observed. These studies reveal olfactory receptors on TPB antennae responsive to insect and host-plant volatiles that are likely to play a role in host finding and sexual attraction.

Key Words—*Lygus lineolaris*, olfaction, pheromone, host odor, electroantennogram, EAG, butyrates, green odor, host finding, sex attraction.

INTRODUCTION

The tarnished plant bug (TPB), *Lygus lineolaris* (Palisot de Beauvois), is a serious pest recorded on 169 plant species belonging to 36 families in the Mis-

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Mississippi River delta of Mississippi, Louisiana, and Arkansas (Snodgrass et al., 1984). TPBs proliferate in spring on a variety of weeds with successive generations often migrating to cotton and other economically important crops (Womack and Schuster, 1987; Fleischer and Gaylor, 1987) where they cause damage by feeding on growing terminals and fruiting buds (Scales and Furr, 1968). Insecticide application on cotton to contain TPB populations also reduces numbers of parasites and predators, which allows other cotton pests, such as the tobacco budworm, *Heliothis virescens* (Fabr.), to reach economic damage levels (Gueldner and Parrott, 1978).

Synthetic attractants for *Lygus* bugs could play an important role in management programs of these polyphagous pests. The attraction of TPB males to traps baited with virgin females was first demonstrated in the field by Scales in 1968, and later by Blumenthal (1978) and Slaymaker and Tugwell (1984). Attraction of males by conspecific and congeneric females was studied by Graham (1987) in four *Lygus* spp.: *L. lineolaris*, *L. hesperus*, *L. desertinus*, and *L. elisus*. In sexual attraction studies of *L. hesperus*, removal of antennal flagella of males or isolating them from female odors eliminated attraction of males to females (Graham, 1988). Female TPBs contain equivalent amounts of *n*-hexyl butyrate and (*E*)-2-hexenyl butyrate, but males contain much less of the unsaturated ester (Gueldner and Parrott, 1978). Field responses of TPBs to these and other esters were not statistically significant (Hedin et al., 1985). Another study of airborne extracts demonstrated sexual dimorphism in which the ratio of (*E*)-2-hexenol to 1-hexanol appears to be greater than the relative differences in the concentrations of esters in males and females (Aldrich et al., 1988).

The neural basis of reception of plant odors and pheromone components by Hemiptera is poorly known. Olfactory responsiveness of a single neuron of *Triatoma infestans* to human breath was the first report on bug olfaction (Mayer, 1968). Electrophysiological studies on *Oncopeltus fasciatus* revealed that adult milkweed bugs have olfactory receptors on their antennae that respond to host plant odors (Pantle and Feir, 1976). The purpose of this study was to use electroantennograms (EAGs) to investigate peripheral olfactory responsiveness of adult *L. lineolaris* to potent pheromones and plant odors. This investigation was further intended to provide a basis for studies of single-receptor neuron responses of TPBs.

METHODS AND MATERIALS

Insects. Adults of *Lygus lineolaris* were obtained from a laboratory colony maintained at the USDA, Southern Insect Management Laboratory, Stoneville, Mississippi. Upon arrival, insects were segregated by sex, placed in separate plastic cups, and fed broccoli florets. Insects were held in an incubator pro-

grammed at 25°C to darkness. The sexes

Olfactory Stimuli. Purities are listed in presence in *L. lineolaris* dilutions in nanograms (mm long × 5 mm wide × 18 mm). These were 1 cm. Odor molecule preparation by dry, was 1 sec during the studies. Interstimulus EAG. The atmospheric Because of the variations can be made in pounds.

Electrophysiology. Techniques utilized in the by Schneider (1957) and Payne, 1977, filled with *Drosophila* cork block using a distal region of the was positioned into puncturing with an amplified 100× by Tektronix 5111A Instruments strip-chart

Experimental. of the antennal receptor two series of experiments the general response was measured by the load of each. Presentation.

In the second examination based on were constructed from (0.001–100 µg/µl) the highest dose. Sexes (females) were recorded filter paper impreg-

ouisiana, and Arkansas (Snodgrass et al., a variety of weeds with successive generations and other economically important crops (Pether and Gaylor, 1987) where they cause damage to fruiting buds (Scales and Furr, 1988). The presence of TPB populations also reduces the damage which allows other cotton pests, such as *Scirpophaga* (Fabr.), to reach economic damage

bugs could play an important role in managing cotton pests. The attraction of TPB males to females was first demonstrated in the field by Scales (1988) and Slaymaker and Tugwell (1984). The attraction of conspecific females was studied by Grainger (1988) for *L. lineolaris*, *L. hesperus*, *L. desertinus*, and *L. hesperus*, removal of antennal flagella eliminated attraction of males to females. TPBs contain equivalent amounts of *n*-hexyl acetate but males contain much less of the unsaturated compounds (78). Field responses of TPBs to these and other compounds (Hedin et al., 1985). Another study of sexual dimorphism in which the ratio of (*E*)- β -caryophyllene was greater than the relative differences in the responses of females (Aldrich et al., 1988).

plant odors and pheromone components. The electrophysiological responsiveness of a single neuron of the antenna was the first report on bug olfaction (Mayer, 1988). *Oncopeltus fasciatus* revealed that adult males have neurons on their antennae that respond to host plant odors. The purpose of this study was to use electrophysiology to investigate peripheral olfactory responsiveness to pheromones and plant odors. This investigation is for studies of single-receptor neuron

AND MATERIALS

Insects were obtained from a laboratory colony of the Texas A&M Insect Management Laboratory, Stoneville, Mississippi. Insects were segregated by sex, placed in separate cages. Insects were held in an incubator pro-

grammed at 25°C temperature and a photoregime of 14 hr of light and 10 hr of darkness. The sexes were separated for at least two days prior to use.

Olfactory Stimuli. Odorants used as olfactory stimuli, their sources and purities are listed in Table 1. Test compounds were selected based on their presence in *L. lineolaris* or its host plants (see Table 1 for references). Stimulus dilutions in nanograde hexane were delivered from glass odor cartridges (80 mm long \times 5 mm ID) as 1- μ l aliquots on Whatman No. 1 filter paper (7 mm \times 18 mm). These odor cartridges were oriented towards the preparation from 1 cm. Odor molecules evaporating from the filter paper were carried over the preparation by dry, charcoal-filtered, hydrocarbon-free air. Stimulus duration was 1 sec during the first series of experiments, and 0.5 sec for dose-response studies. Interstimulus time intervals of 2–3 min allowed for recovery of the EAG. The atmosphere around the preparation was continuously exhausted. Because of the variation in volatility of test compounds, only relative comparisons can be made between the odorous stimuli except for closely related compounds.

Electrophysiological Recording System. Electroantennogram (EAG) techniques utilized in these studies were a modification of a previous technique used by Schneider (1957a) and are described in detail elsewhere (Payne, 1970; Dickens and Payne, 1977; Dickens, 1984). In general, Ag–AgCl capillary electrodes filled with *Drosophila* Ringer were used. Intact bugs were immobilized on a cork block using adhesive tape. The recording electrode was inserted into the distal region of the terminal antennal segment, while the indifferent electrode was positioned into the scape. The electrodes were placed into the antenna after puncturing with an electrolytically sharpened tungsten wire. The signal was amplified 100 \times by a Grass P-16 microelectrode DC amplifier and viewed on a Tektronix 5111A storage oscilloscope. EAGs were recorded on a Houston Instruments strip-chart recorder.

Experimental Protocol. In order to elucidate the selectivity and sensitivity of the antennal receptors of the TPB for potential pheromones and plant odors, two series of experiments were performed. In the first series of experiments, the general responsiveness of the antennal receptors to the individual odorants was measured by recording EAGs to volatiles emanating from a 100- μ g stimulus load of each. Presentation of each odorant was randomly ordered for each preparation.

In the second series of experiments, nine odorants were selected for closer examination based on data obtained in initial experiments. Dose-response curves were constructed from EAGs elicited by serial dilutions of each compound (0.001–100 μ g/ μ l). Serial dilutions were presented in order from the lowest to the highest dose. Six replicates for each sex (12 insects total, six males and six females) were recorded for both experimental series. Control stimulations (using filter paper impregnated with 1 μ l of the hexane solvent) were made at the

TABLE 1. SOURCE, PURITY, AND BIOLOGICAL PRESENCE OF ODOROUS STIMULI USED IN ELECTROPHYSIOLOGICAL EXPERIMENTS

Compound	Source of supply ^a	Chemical purity (%)	Identified from insect (I) or host plant (P) ^b
Butyrates			
Ethyl butyrate	A	>99	I 1, 2
(E)-2-Hexenyl butyrate	B	>99	I 1, 2
Butyl butyrate	C	>99	I 1, 2
Hexyl butyrate	C	>99	I 1, 2
Green leaf volatiles			
(E)-2-Hexenal	A	>99	I 2 P 2, 4, 5 in cotton buds
(Z)-3-Hexenal	A	>99	P 2, 4, 5 in buds I 2
(E)-2-Hexenyl acetate	A	>99	I 1, 2
Hexyl acetate	A	>99	I 1, 2
Benzenoids	A		
Phenylacetaldehyde	A	>99	I 2, 5 P 2, 3 in mustard and corn silks
Benzaldehyde	A	>98	P 4, 5 in buds
Monoterpenes			
(±)-linalool	A	>99	P 4, 5 in buds
(-)-linalool	D	>99	
Geraniol	E	71	P 4, 5 in buds
Nerol	E	64.2	P, 5 in buds
(±)- α -Pinene	A	>99	P 3, 4, 5 cotton bud oil and golden rod
(-)-Limonene	A	>99	
(+)-Limonene	A	>99	P 3, 4, 5 cotton bud oil, croton and golden rod
Myrcene	A	85	P 4, 5 bud oil
Aliphatic alcohols			
1-Heptanol	A	90-95	
1-Octanol	A	85-90	P 5 bud
1-Nonanol	A	80-90	P 5 bud
1-Decanol	A	>99	
Aliphatic aldehydes			
Heptanal	A	70-75	P 4, 5 buds
Octanal	A	75-80	
Nonanal	A	80-85	P 4, 5 buds
Decanal	A	95	P 5 buds
Other compounds			
Ethyl hexanoate	A	>99	I 1, 2
Ethyl (E)-2-hexenoate	A	>99	I 1, 2
Ethyl myristate	A	>99	I 1
Butylacetate	A	>99	I 1, 2

^aA, Aldrich Chem. Co., Milwaukee, Wisconsin; B, Bedoukian Research Inc., Danbury, Connecticut; C, synthesized by Jan Kochansky, USDA, ARS, INHL, Beltsville, Maryland; D, K&K Laboratories, Inc., Cleveland, Ohio; E, Pfaltz & Bauer, Inc., Stamford, Connecticut.

^b1 = Aldrich et al. (1988); 2 = Gueldner and Parrot (1978); 3 = Gueldner and Parrot (1981); 4 = Hedin et al. (1973); 5 = Hedin et al. (1976).

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beginning and at the was subtracted from

1-Hexanol (100- all responses, so the (Payne, 1975) could followed every two percentages of the mean (1978, 1981). Maximum initial 500 msec of recordings. Hyperpolarization as zero responses for ionization was considered acceptors (receptor Payne, 1977).

Definitions of the tions (Dickens, 1981) dose at which the mean as the highest dose succeeding dose.

Statistical Analysis of variance procedure (Snedecor, 1955). Sexual responses compared for significance (Ostle, 1969).

Mean responses significantly different between 0.173 mV) for 29 min

Selectivity

In general, results populations for the between the sexes in cases were the different

Response to Butylacetate significantly greater than in both the sexes. Mean were equivalent and, however, no significant differences esters at the 100- μ g

Chemical purity (%)	Identified from insect (I) or host plant (P) ^b
> 99	I 1, 2
> 99	I 1, 2
> 99	I 1, 2
> 99	I 1, 2
> 99	I 2 P 2, 4, 5 in cotton buds
> 99	P 2, 4, 5 in buds I 2
> 99	I 1, 2
> 99	I 1, 2
> 99	I 2, 5 P 2, 3 in mustard and corn silks
> 98	P 4, 5 in buds
> 99	P 4, 5 in buds
> 99	P 4, 5 in buds
71	P 4, 5 in buds
64.2	P, 5 in buds
> 99	P 3, 4, 5 cotton bud oil and golden rod
> 99	P 3, 4, 5 cotton bud oil, croton and golden rod
> 99	P 4, 5 bud oil
85	P 4, 5 bud oil
90-95	
85-90	P 5 bud
80-90	P 5 bud
> 99	
70-75	P 4, 5 buds
75-80	
80-85	P 4, 5 buds
95	P 5 buds
> 99	I 1, 2
> 99	I 1, 2
> 99	I 1
> 99	I 1, 2

^b B. Bedoukian Research Inc., Danbury, Connect-
A, ARS, INHL, Beltsville, Maryland; D, K&K
& Bauer, Inc., Stamford, Connecticut.
Parrot (1978); 3 = Gueldner and Parrot (1981);
'6).

beginning and at the end of each preparation. The mean response to the control was subtracted from each EAG.

1-Hexanol (100- μ g stimulus load) was used as a standard for normalizing all responses, so that responses within an individual and among individuals (Payne, 1975) could be compared. Stimulation with the standard preceded and followed every two stimulations. Millivolt responses were converted into percentages of the mean of the two nearest responses to the standard (Dickens, 1978, 1981). Maximal EAG depolarizations, which usually occurred during the initial 500 msec of the stimulation period, were measured from strip-chart recordings. Hyperpolarizations, as observed for some chemicals, were treated as zero responses for statistical purposes. The magnitude of the EAG depolarization was considered to be a measure of the relative number of responding acceptors (receptor sites) (Kaissling, 1971, 1974; Payne, 1975; Dickens and Payne, 1977).

Definitions of threshold and saturation were modified from earlier definitions (Dickens, 1981, 1984). The threshold was considered to be the lowest dose at which the mean response increased, while the saturation level was taken as the highest dose at which the mean response was equal to or less than the succeeding dose.

Statistical Analyses. EAGs were compared statistically using the analysis of variance procedure and Duncan's multiple-range mean separation test (Duncan, 1955). Sexual differences between points on dose-response curves were compared for significant differences in sexes using the *t* test for two means (Ostle, 1969).

RESULTS

Mean responses of *L. lineolaris* to the 1-hexanol standard were not significantly different between males (-1.74 ± -0.147 mV) and females (-1.61 ± 0.173 mV) for 29 males and 31 females, respectively.

Selectivity

In general, results indicated significant differences in the size of acceptor populations for the various compounds tested. Although slight differences between the sexes in EAGs to each of the odorants were noted, in only a few cases were the differences significant.

Response to Butyrates. EAGs elicited by the hexyl butyrates were significantly greater than those elicited by either ethyl or butyl butyrate (Figure 1A) in both the sexes. Male responses to (*E*)-2-hexenyl butyrate and hexyl butyrate were equivalent and were greater than female responses to these esters. However, no significant differences were found between responses of either sex to esters at the 100- μ g stimulus load.

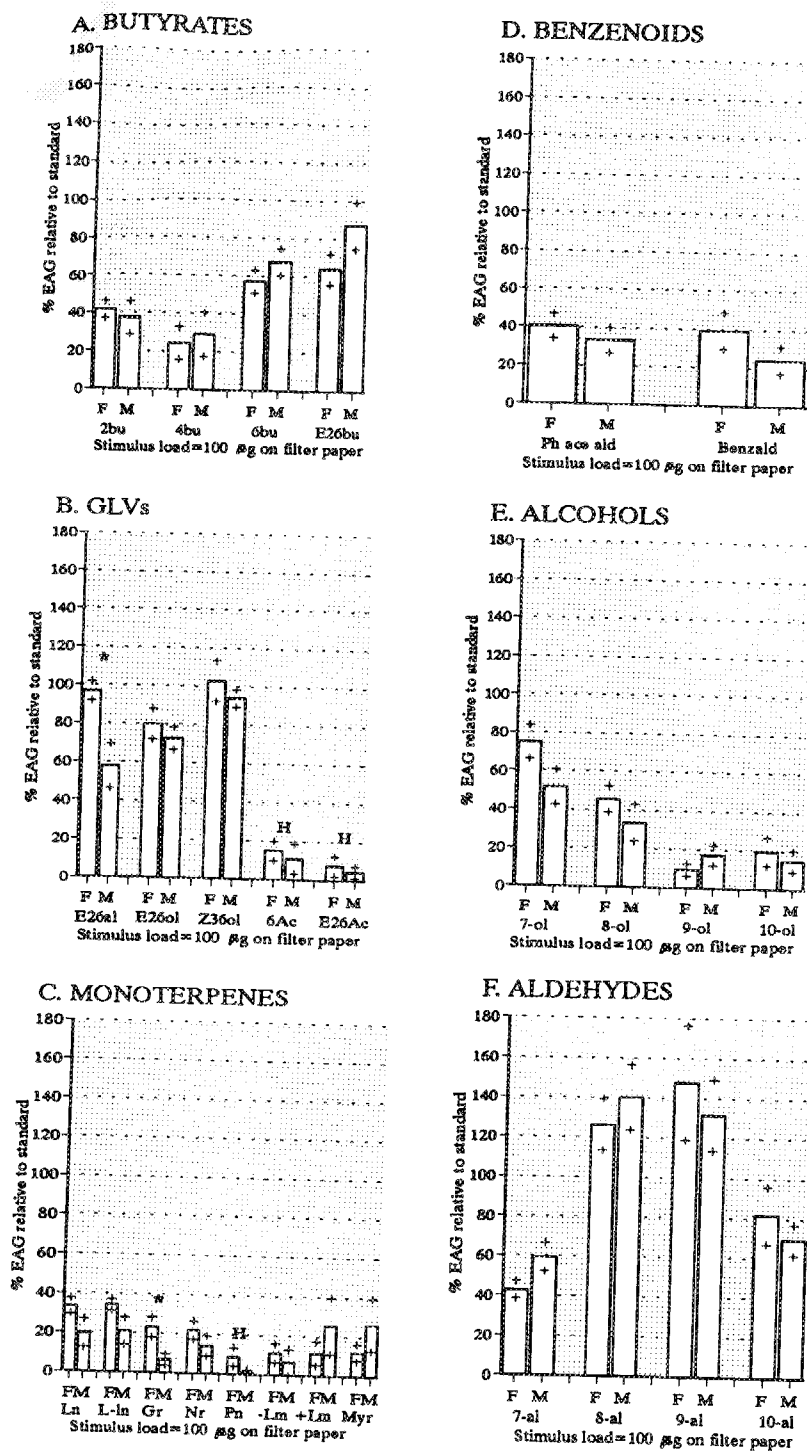


FIG. 1. Mean EAGs for selected insect and human odors: 2bu = butyrate; 6bu = hexyl butyrate; E26al = (E)-2-hexyl acetate; E26ol = (E)-2-hexyl octyl acetate; L-ln = (-)-linalool; Ph ace ald = phenyl acetate; 7-ol = heptanol; 8-ol = octanol; 9-ol = nonanol; 10-ol = decanol; E6ate = ethyl hexanoate; Bace = butyl acetate. * indicates significant difference between F and M.

Response to six carbon aldehydes
elicited by corresponding odors were significantly different in responses by (Z)-3-hexenol.

Response to odors in EAGs by both sexes
was observed in (±)-linalool, and hydrocarbons. EAGs were observed in EAGs were observed

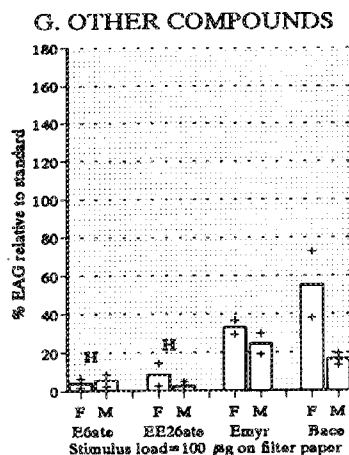
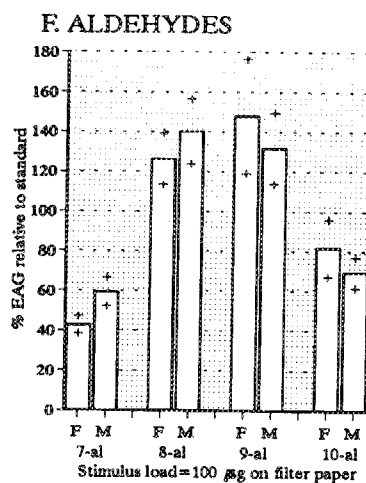
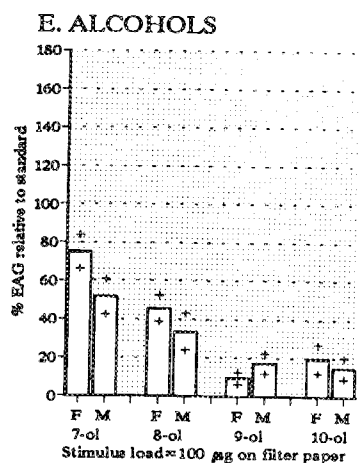
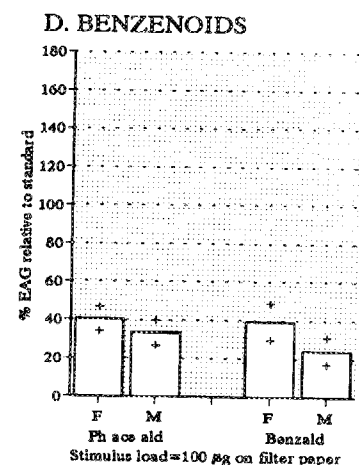


FIG. 1. Mean EAGs of male and female *Lygus lineolaris* to 100-µg stimulus loads of selected insect and plant odorants: (A) butyrates (2bu = ethyl butyrate; 4bu = butyl butyrate; 6bu = hexyl butyrate; E26bu = (*E*)-2-hexenyl butyrate); (B) GLVs (leaf volatiles [E26al = (*E*)-2-hexenal; E26ol = (*E*)-2-hexenol; Z36ol = (*Z*)-3-hexenol; 6Ac = hexyl acetate; E26Ac = (*E*)-2-hexenyl acetate]; (C) monoterpenes [Ln = (\pm)-linalool; L-ln = ($-$)-linalool; Gr = geraniol; Nr = nerol; Pn = (\pm)- α -pinene]; (D) benzenoids (Ph ace ald = phenylacetaldehyde; benzald = benzaldehyde); (E) alcohols (7-ol = heptanol; 8-ol = octanol; 9-ol = nonanol; 10-ol = decanol); (F) aldehydes (7-al = heptanal; 8-al = octanal; 9-al = nonanal; 10-al = decanal); (G) other compounds [E6ate = ethyl hexanoate; EE26ate = ethyl (*E*)-2-hexenoate; Emyr = ethyl myristate; Bace = butyl acetate]. A plus sign above and below bars represents \pm SE; *Significant sexual difference, $P < 0.05$, t test for two means. H indicates odorant often produced hyperpolarization of EAG.

Response to Green Leaf Volatiles (GLVs). Mean EAGs from females to six carbon aldehydes and alcohols were significantly greater than the EAGs elicited by corresponding six carbon acetates. EAGs elicited by (*E*)-2-hexenal were significantly greater for females than males (Figure 1B). Although differences in responses between the sexes were not significant, the response elicited by (*Z*)-3-hexenol was the highest among five compounds tested in this group.

Response to Monoterpenes. Although there are no significant differences in EAGs by both sexes to individual monoterpenes, a relatively greater response was observed in females to oxygenated monoterpenes [($-$)-linalool, racemic (\pm)-linalool, and the geometric isomers geraniol and nerol] than to monoterpene hydrocarbons. EAGs elicited by geraniol in females were significantly greater than those elicited in males (Figure 1C). Occasionally hyperpolarizations of the EAGs were observed for stimulation with monoterpene hydrocarbons.

Response to Benzenoids. Although no significant differences in EAGs were noted between the sexes and among the individual benzenoids (Figure 1D), EAGs recorded from females to both aromatic compounds were greater than those recorded from males.

Response to Aliphatic Alcohols and Aldehydes. EAGs to primary alcohols decreased with increasing carbon chain length (Figure 1E). EAGs elicited by aldehydes of increasing chain length increased to a maximum at eight or nine carbons before declining with the 10-carbon compound for both sexes (Figure 1F).

Response to Other Compounds. Butyl acetate and ethyl myristate elicited depolarizing EAGs. Ethyl hexanoate and ethyl (*E*)-2-hexenoate elicited hyperpolarizations. Butyl acetate elicited maximal EAGs among compounds in this group (Figure 1G). However, no significant sexual differences were found.

Sensitivity

In general, after reaching threshold, responses to the compounds tested increased with increasing stimulus loads until saturation. Dose-response curves for EAGs of males and females to 1-hexanol were almost identical (Figure 2A). Saturation was not reached by either sex even at the 1000- μ g dose.

For convenience the odorants tested in dose-response studies were grouped into two categories: insect-produced compounds and plant volatiles.

Insect-Produced Compounds. In general, the dose-response curves constructed from EAGs elicited by compounds present in insects were similar in shape. To the compounds (*E*)-2-hexenyl butyrate and hexyl butyrate, male *Lygus* receptors responded similarly in reaching threshold and saturation levels at the same doses tested. Statistically significant differences were observed between the sexes at the 10- μ g dose, where the responses reached saturation level for both sexes (Figure 2B and C). EAGs elicited by butyl acetate in both females and males at the intermediate doses tested (0.1 and 1.0 μ g) were significantly different (Figure 2D). However, responses at higher doses tested were nearly the same, and the curves showed an increasing trend in both the sexes.

Plant Volatiles. Some of the plant volatiles were also reported in small amounts in *Lygus* adults (Table 1). Generally, the green leaf volatiles, (*Z*)-3-hexenol, (*E*)-2-hexenol, and (*E*)-2-hexenal, elicited greater EAGs than any other odors tested in both sexes. Male EAGs to (*E*)-2-hexenol and (*E*)-2-hexenal were significantly greater than those of females at the 100- μ g and 0.01- μ g doses tested, respectively (Figure 2F and G). Dose-response curves constructed from the EAGs to (*Z*)-3-hexenol in both the sexes were identical (Figure 2E).

The oxygenated monoterpene, geraniol, which elicited significantly greater response by females than males in selectivity studies, also elicited significantly greater EAGs by females in dose-response studies. Females reached threshold

earlier (0.01- μ g dose) and elicited greater EAGs to 10- μ g dose than to increasing stimulus loads above threshold in both sexes tested in bugs and as well in bees.

Nonanal, a known sex attractant of *Lygus* spp. (Borden, personal communication), was tested in the experimental series. Dose-response curves were similar in both sexes, while males reached threshold at a 10- μ g dose. However, the differences were statistically insignificant.

Selectivity

The similarity in response to different chemical cues in locusts may be explained by the fact that locusts are generalist feeding insects (Fein et al., 1988; Hansson et al., 1992).

In general, EAGs increased with increasing chain length of the compounds tested. (*E*)-2-hexenyl butyrate and hexyl butyrate elicited the highest EAGs. This correlates with the fact that hexenyl butyrate is the most abundant compound detected in locusts (Aldrich et al., 1978; Aldrich et al., 1988). The compounds detected in locusts are similar to those detected in green leaf volatiles (GLV) based on its gross composition (1:1 ratios). The sex differences in response to (*E*)-2-hexenol and (*E*)-2-hexenal, may indicate pheromonal attraction. The response of *L. hesperus* revealed that the sex difference is not sexually dimorphic. The response of *L. hesperus* is similar to that of *L. fasciatus* (Dallas): males

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earlier (0.01- μ g dose) than males (0.1 μ g), and responded with significantly
greater EAGs to 10- μ g and 100- μ g doses (Figure 2H). Dose-response curves
to increasing stimulus loads of phenylacetaldehyde increased after reaching the
threshold in both sexes (Figure 2I). This aromatic compound was reported both
in bugs and as well in host plants (see references in Table 1).

Nonanal, a known plant volatile that was recently identified from another
Lygus spp. (Borden, personal communication), elicited greater EAGs than any
other compound tested. Females responded greatly to this odorant in both exper-
imental series. Dose-response curves show similarity in reaching the thresholds
in both sexes, while male antennae appeared to have reached saturation at the
10- μ g dose. However, the differences in EAGs between the sexes were statisti-
cally insignificant.

DISCUSSION

Selectivity

The similarity in EAGs of male and female *L. lineolaris* to plant odors
may be explained by their common habitat, where they may utilize the same
chemical cues in locating the host plants on which they feed and mate (Li et
al., 1992). Similar results were obtained in previous studies with other plant-
feeding insects (Fein et al., 1982; Dickens, 1984; Wellso et al., 1984; Light et
al., 1988; Hansson et al., 1989).

In general, EAGs to butyl esters for males and females increased with
increasing chain length of the parent acid moiety. The acceptor populations for
(*E*)-2-hexenyl butyrate and hexyl butyrate in males were greater than in females.
This correlates with the fact that females contain relatively much more (*E*)-2-
hexenyl butyrate in their scent glands than do males (Gueldner and Parrott,
1978; Aldrich et al., 1988). Gueldner and Parrott (1978) reported that most of
the compounds detected in their studies from TPB were esters. They also sug-
gested (*E*)-2-hexenyl butyrate could be an important component of the sex pher-
omone based on its greater abundance in females than in males. They observed
(*E*)-2-hexenyl butyrate and hexyl butyrate in male and female TPBs at 10:1
and 1:1 ratios. The sexual dimorphism observed in EAGs of *L. lineolaris* males
and females to (*E*)-2-hexenyl butyrate and hexyl butyrate, and their presence in
females, may indicate the involvement of these compounds in the process of
pheromonal attraction. However, a comparative study of *L. lineolaris*, *L. elisus*,
and *L. hesperus* revealed that the ratio of (*E*)-2-hexenyl butyrate to hexyl butyr-
ate is not sexually dimorphic in *L. hesperus*, whereas in *L. elisus* this ester
dimorphism is similar to that for *L. lineolaris* (Aldrich et al., 1988). Games and
Staddon (1973) demonstrated sexual dimorphism of chemicals in *Oncopeltus*
fasciatus (Dallas): male scent consisted of acetates, while female scent was

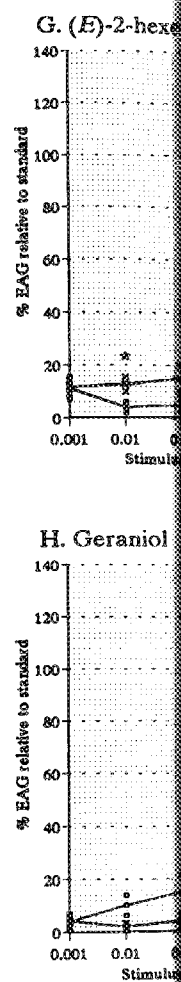
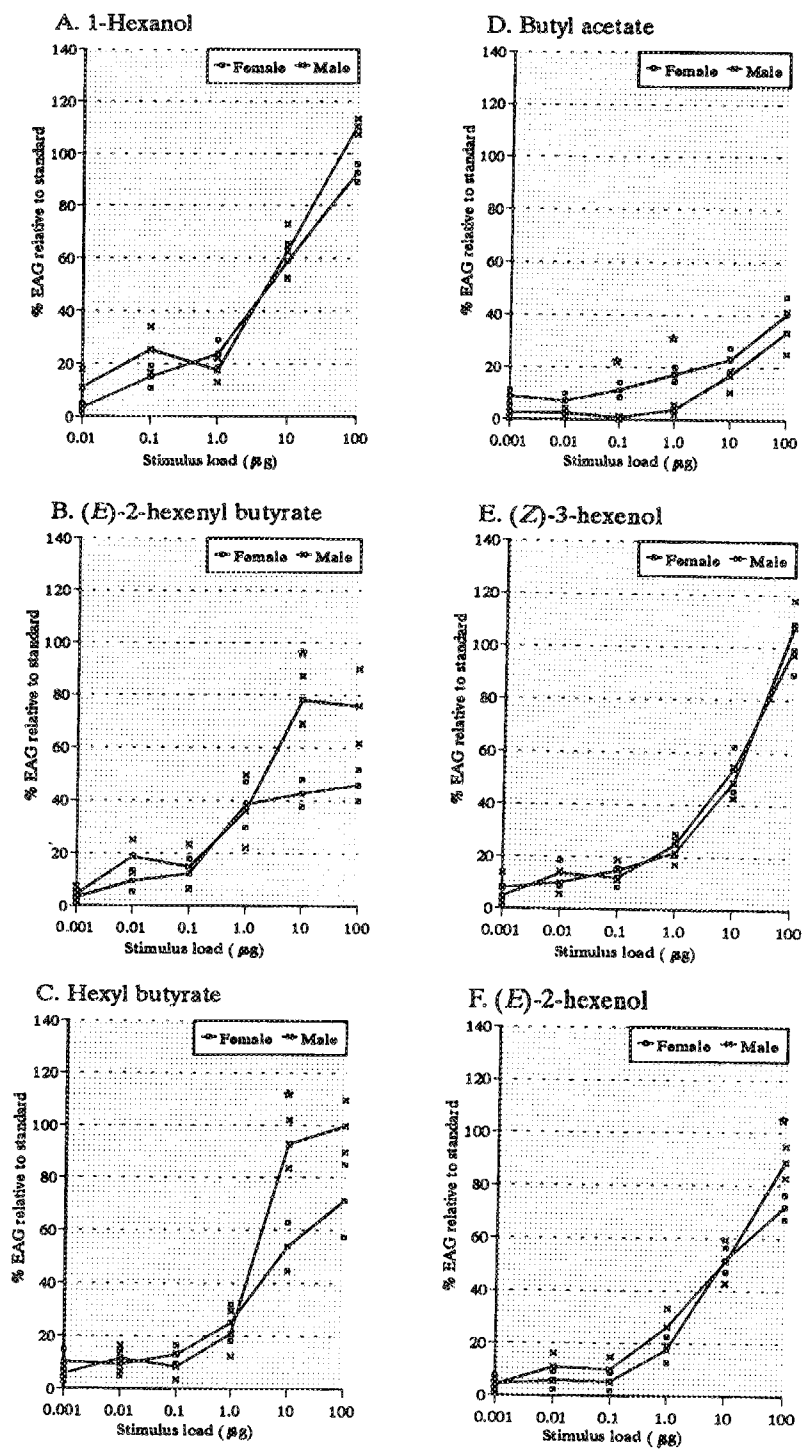


FIG. 2. Dose-response curves for serial stimulation in female and male subjects for various chemical stimuli. (A) 1-Hexanol, (B) (E)-2-hexenyl butyrate, (C) Hexyl butyrate, (D) Butyl acetate, (E) (Z)-3-hexenol, (F) (E)-2-hexenol, (G) (E)-2-hexenol, (H) Geraniol. Markers above and below the lines represent individual data points. □ = females. *Significant difference between sexes.

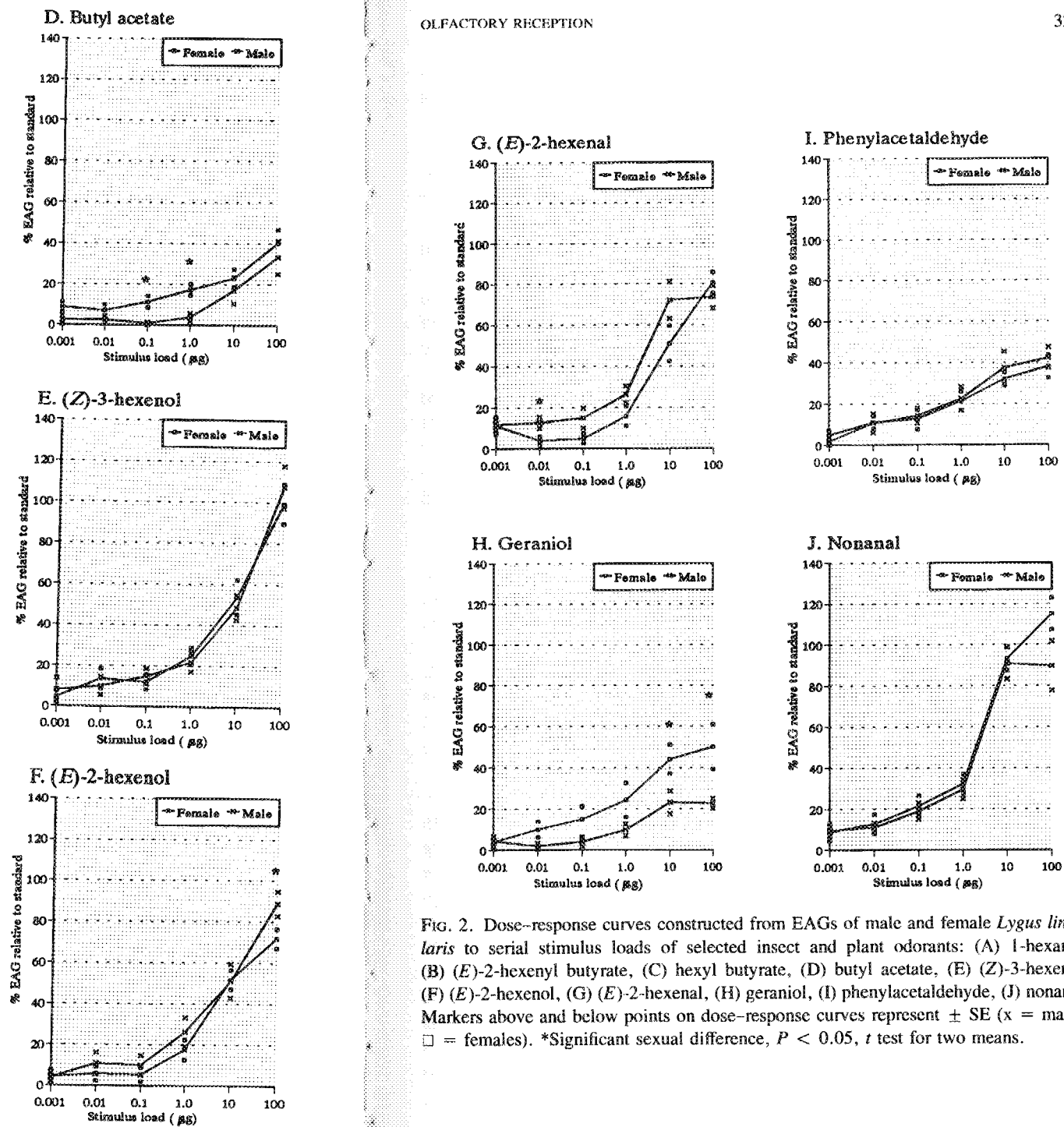


FIG. 2. Dose-response curves constructed from EAGs of male and female *Lygus lineolaris* to serial stimulus loads of selected insect and plant odorants: (A) 1-hexanol, (B) (E)-2-hexenyl butyrate, (C) hexyl butyrate, (D) butyl acetate, (E) (Z)-3-hexenol, (F) (E)-2-hexenol, (G) (E)-2-hexenal, (H) geraniol, (I) phenylacetaldehyde, (J) nonanal. Markers above and below points on dose-response curves represent \pm SE (x = males; □ = females). *Significant sexual difference, $P < 0.05$, t test for two means.

mostly aldehydes. They attributed these differences to the tubular glands of the scent gland complex, which were larger in males than in females. Similar sexual dimorphism was noted in the giant water bug *Lethocerus indicus* for (*E*)-2-hexenyl butyrate (Devakul and Maarse, 1964).

Greater EAGs of females to six-carbon aldehyde and alcohols, i.e., GLVs, may be attributed to their role in host orientation (Visser et al., 1979, Visser and Avé, 1978; Visser, 1983). (*E*)-2-Hexenal, (*Z*)-3-hexenol, and (*E*)-2-hexenol were reported in cotton buds (Hedin et al., 1973, 1976). (*E*)-2-Hexenal and (*Z*)-3-hexenol were also identified in TPB (Gueldner and Parrott, 1978). EAGs recorded in response to these compounds are comparable with those obtained for several other insect species (Visser, 1983) including the oak leaf weevils, *Rhychaenus quercus* L. (Kozlowski and Visser, 1981), which were most responsive to both the six-carbon alcohols and aldehydes.

In general, *Lygus* bugs had more acceptors responsive to the oxygenated monoterpenes than to the monoterpene hydrocarbons. Greater responsiveness at the EAG level to oxygenated monoterpenes versus monoterpene hydrocarbons has been observed in several phytophagous insects [Visser (1979) in *Leptinotarsa decemlineata*; Kozlowski and Visser (1981) in *R. quercus*; Guerin and Visser (1980) in *Psila rosae*; and Dickens (1984) in *Anthonomus grandis*].

Benzenoids elicited significant EAGs in both female and male TPBs. Benzaldehyde was reported in cotton buds (Hedin et al., 1973, 1976). Phenyl acetaldehyde was found in TPB and mustard plants (Gueldner and Parrott, 1978, 1981). Cantelo and Jacobson (1979) reported phenylacetaldehyde in corn silk and found it to be attractive to TPBs in the field.

A general decrease in EAG response with increasing chain length for aliphatic alcohols and increase in EAG responsiveness to the increasing chain length of aliphatic aldehydes through nine carbons was found in both the sexes. The fact that EAGs elicited by aldehydes were sometimes greater than for the corresponding alcohols may be due to their higher volatility. However, volatility of both alcohols and aldehydes decrease with increasing carbon chain length. Thus, decreasing EAGs to the primary alcohols with increasing chain length corresponds with the decreasing volatility of these compounds. The increasing EAGs to aldehydes of increasing chain length may only be explained by a greater affinity of antennal receptors for these molecules since fewer molecules evaporating from the filter paper would be available for interaction with the acceptors. Nonanal was reported from cotton (Hedin et al., 1973, 1976), and more recently was identified by coupled gas chromatography (GC) -electroantennographic analysis and coupled GC-mass spectrometry as a potential semiochemical in volatiles captured from female TPBs feeding on bean pods, *Phaseolus vulgaris* L. (Pierce, Gries, Wardle and Borden, personal communication). Greater EAGs to this compound and its presence in both plants and bugs indicates that this compound may be of significance in both pheromonal attraction and host finding.

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Seven-carbon aldehyde and alcohols, i.e., GLVs, are important for host orientation (Visser et al., 1979, Visser et al., 1983). (*E*)-2-Hexenal, (*Z*)-3-hexenol, and (*E*)-2-hexenal are important for host orientation (Hedlin et al., 1973, 1976). (*E*)-2-Hexenal is found in TPB (Gueldner and Parrott, 1978). These compounds are comparable with those found in other species (Visser, 1983) including the oak leaf miner (*Lithocolpa* sp.) (Kozłowski and Visser, 1981), which were found on alcohols and aldehydes.

More acceptors responsive to the oxygenated compounds than to the hydrocarbons. Greater responsiveness to terpenes versus monoterpene hydrocarbons was observed in phagous insects [Visser (1979) in *Leptinotarsus*; Visser (1981) in *R. quercus*; Guerin and Dickens (1984) in *Anthonomus grandis*].

EAGs in both female and male TPBs. Ben-Zur et al. (Hedlin et al., 1973, 1976). Phenyl acetate was found in mustard plants (Gueldner and Parrott, 1978, 1980). They reported phenylacetaldehyde in corn silk in the field.

Response with increasing chain length for aliphatic compounds. Greater responsiveness to the increasing chain length of compounds with nine carbons was found in both the sexes. Responses were sometimes greater than for the compounds with higher volatility. However, volatility decreases with increasing carbon chain length. Primary alcohols with increasing chain length showed a decrease in volatility of these compounds. The increasing chain length may only be explained by a greater number of molecules since fewer molecules evaporate available for interaction with the acceptors. Hedlin et al., 1973, 1976), and more recently by gas chromatography (GC) -electroantennographic (EAG) as a potential semiochemical in host finding. Feeding on bean pods, *Phaseolus vulgaris* (L.), (personal communication). Greater EAGs were found in both plants and bugs indicates that this compound is involved in both pheromonal attraction and host finding.

A similar increase in response to seven- to nine-carbon aldehydes was reported in both the honeybee, *Apis mellifera* (Dickens et al., 1986), and the wax moth, *Galleria mellonella* (Payne and Finn, 1977), in which nonanal functioned as a component of its male-produced sex attractant.

Hyperpolarizations were frequently noted while testing the compounds (*E*)-2-hexenyl acetate, hexyl acetate, ethyl hexanoate, ethyl (*E*)-2-hexenoate and (\pm)- α -pinene. Positive polarity receptor potentials defined as hyperpolarizations by Boeckh et al. (1965) and Kaissling (1971) had been observed previously by Schneider (1957a,b). They considered this type of waveform to be due to the inhibition (i.e., decreased action potential frequency) in receptor neurons when stimulated with certain acid compounds. Light et al. (1988) also recorded hyperpolarizations in medfly antennae when stimulated with some short-chain carboxylic acids. Ethyl hexanoate, ethyl (*E*)-2-hexenoate, and ethyl myristate were identified by Gueldner and Parrott (1978) in *Lygus* bugs. None of these compounds were attractive when presented individually in field tests (Hedlin et al., 1985).

Sensitivity

In general, dose-response curves constructed from EAGs of male and female to the compounds revealed males to be more sensitive than the females to many odorants tested. Different thresholds and saturation levels observed for the various odorants in electrophysiological studies might be indicative of the role of each compound in host selection and pheromonal attraction. As reported in previous studies (Dickens et al., 1984), a low threshold for a given compound might indicate the ability of the insect to detect the compound in low concentration at greater distances from its source.

Insect-Produced Compounds. Dose-response curves constructed from EAGs to serial stimulus loads of the esters hexyl butyrate and (*E*)-2-hexenyl butyrate revealed males to be more responsive than females to both odorants (Figure 2B and C). The similar shapes of the dose-response curves for both odorants indicate similar receptor mechanisms for each. Reports by Gueldner and Parrott (1978) and Aldrich et al. (1988) on these ester compounds showed both compounds to be present in both sexes. Butyl acetate, which was also identified in TPB by Gueldner and Parrott (1978), elicited significantly greater responses in female antennae (Figure 2D). The acceptor population for this compound is smaller than the previously mentioned six-carbon esters.

Plant Volatiles. Among all the compounds tested, nonanal elicited the greatest EAGs from both male and female antennae, and dose-response curves for both sexes revealed a relatively low threshold (stimulus load = 0.1 μ g) for this compound (Figures 1F and 2J). However, the responses between the sexes were not significantly different. Nonanal was identified as a host plant (cotton)

volatile by Hedin et al. (1973, 1976). Our results indicate that TPBs have the ability to detect this odorant in low concentration, perhaps at greater distances from its source.

While significant EAGs were elicited by all of the GLVs (Visser, 1979) tested, the alcohol and aldehyde derivatives were more active than the acetates (Figure 1B). We realize that what is being compared in our experiments is the number of molecules evaporating from the filter paper within the odor cartridge and reaching the preparation, which will differ for odorants of different volatilities and binding characteristics of the compound to the filter paper. Based on boiling points, the order of volatility of the GLVs should be: 1-hexanal (bp = 128.6°C) > 1-hexanol (bp = 157.5°C) > hexyl acetate (171.5°C). Thus the greater activity of the aldehyde and alcohol derivatives observed may be explained by differences in volatilities among the derivatives. However, it seems unusual that while the boiling points of the alcohol and aldehyde differ by nearly 30°C, similar EAGs are elicited; yet insignificant or hyperpolarizing EAGs are elicited by the acetates, even though the difference in boiling points for the alcohol and acetate is only 14°C. (*Z*)-3-Hexenol was reported as the body constituent of male and female TPBs (Guelldner and Parrott, 1978). (*E*)-2-Hexenol in cotton and (*E*)-2-hexenal in both cotton and TPB were identified (see Table 1). These compounds may play a role in host-plant finding (Visser and Avé, 1978) or enhancement of pheromone responses (Dickens, 1989; Dickens et al., 1990) as shown for other insects.

Female TPBs were more sensitive and responsive to the oxygenated monoterpene geraniol than were males. Geraniol was reported in cotton buds (Hedin et al., 1973, 1976). Since this compound was not detected in *Lygus* bugs of either sex, and a greater number of acceptors in female antennae responded to this compound, it may be hypothesized that females may use this odor in locating food sources or oviposition sites.

Although previous behavioral experiments in the field indicated phenyl-acetaldehyde as a *Lygus* attractant (Cantelo and Jacobson, 1979), only small EAGs were recorded in response to this compound. This indicates a small but behaviorally significant population of receptors for this odorant.

The EAG studies presented here demonstrate TPBs to have receptors for a wide range of insect-produced odors and host-plant volatiles. In the case of hexyl butyrate, (*E*)-2-hexenyl butyrate, and geraniol sexually dimorphic responses were noted. Green leaf volatiles and nonanal were the most active odorants tested in both sexes. These results and concurrent morphological studies provide a basis for single-sensillum recordings already in progress.

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